FLORAL STRUCTURE OF *TAKHTAJANIA* AND ITS SYSTEMATIC POSITION IN WINTERACEAE[1]

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ABSTRACT

Floral structure of *Takhtajania perrieri*, the sole species of Winteraceae in Africa/Madagascar, was studied and compared with that in other Winteraceae. Floral organs are in more or less regular whorls, starting dimerous in the outer perianth region and changing to tetramerous and pentamerous in the inner perianth region and androecium. The innermost androecium whorl is often incomplete. The outer tepal pair is congenitally united, and pairs two and three are postgenitally united in their overlapping area in bud. At the transition from the female to the male phase of anthesis the club-shaped stamen filaments are inflated by cell enlargement, accompanied by starch consumption. The dimerous nature of the unilocular gynoecium is confirmed. The normal linear placentae of the two carpels are oblique to almost horizontal, and therefore the gynoecium does not conform to a usual paracarpous gynoecium with parietal placentation. The ovules are larger than those in other Winteraceae. However, the total evidence of floral features clearly shows the position of *Takhtajania* in the Winteraceae. Within the family it fits best in the *Pseudowintera/Zygogynum*-clade, which is sister to the *Tasmannia/Drimys* clade.

Key words: androecium, floral anatomy, floral morphology, gynoecium, perianth, *Takhtajania*, Winteraceae.

Takhtajania perrieri (Capuron) Baranova & J.-F. Leroy is the sole surviving species of Winteraceae in the Madagascan/African region. It achieved notoriety because of its strange bicarpellate but unilocular gynoecium, which is unique for Winteraceae, a feature that was noticed only 70 years after the discovery of the plant in Madagascar (Leroy, 1977, 1978). For almost 90 years the plant was known only from the type collection of 1909, which contained only scarce floral material, and it was thus thought to be possibly extinct. The rediscovery (re-collected in 1994 and determined in 1997; Schatz et al., 1998) offers the possibility for detailed studies of the disputed floral structure and a comparison with the other genera of Winteraceae.

Since the unusual gynoecium structure of *Takhtajania* has puzzled botanists, it seems appropriate to give a short introductory survey of the previous interpretations. In the original description of *T. perrieri*, the gynoecium was described as unicarpellate (Capuron, 1963). Because of the small floral involucre and the apical anthers with subhorizontal thecae, Capuron (1963) associated the plant with *Bubbia* and placed it into that genus as *Bubbia perrieri*. Baranova (1972) later found that the leaf epidermis of the plant differed from other Winteraceae. It was her suggestion that it could be a separate genus that prompted Leroy (1977, 1978) to restudy the flowers (see also Leroy, 1993). To his surprise, he found the gynoecium to be bicarpellate, syncarpous but unilocular. This was at first questioned by Tucker and Sampson (1979), because its external shape scarcely differs from single carpels of some other Winteraceae. However, Vink (1978) confirmed its bicarpellate nature, but interpreted the two longitudinal furrows of the gynoecium as being dorsal in each carpel (because they alternate with the placentae) and not lateral, as Leroy (1977) contended. This was later also accepted by Leroy (1980) and Deroin and Leroy (1993).

Study of the scarce floral material of the type specimen concentrated on the puzzling gynoecium, whereas the other floral organs received less attention. The aim of the present study is thus to provide

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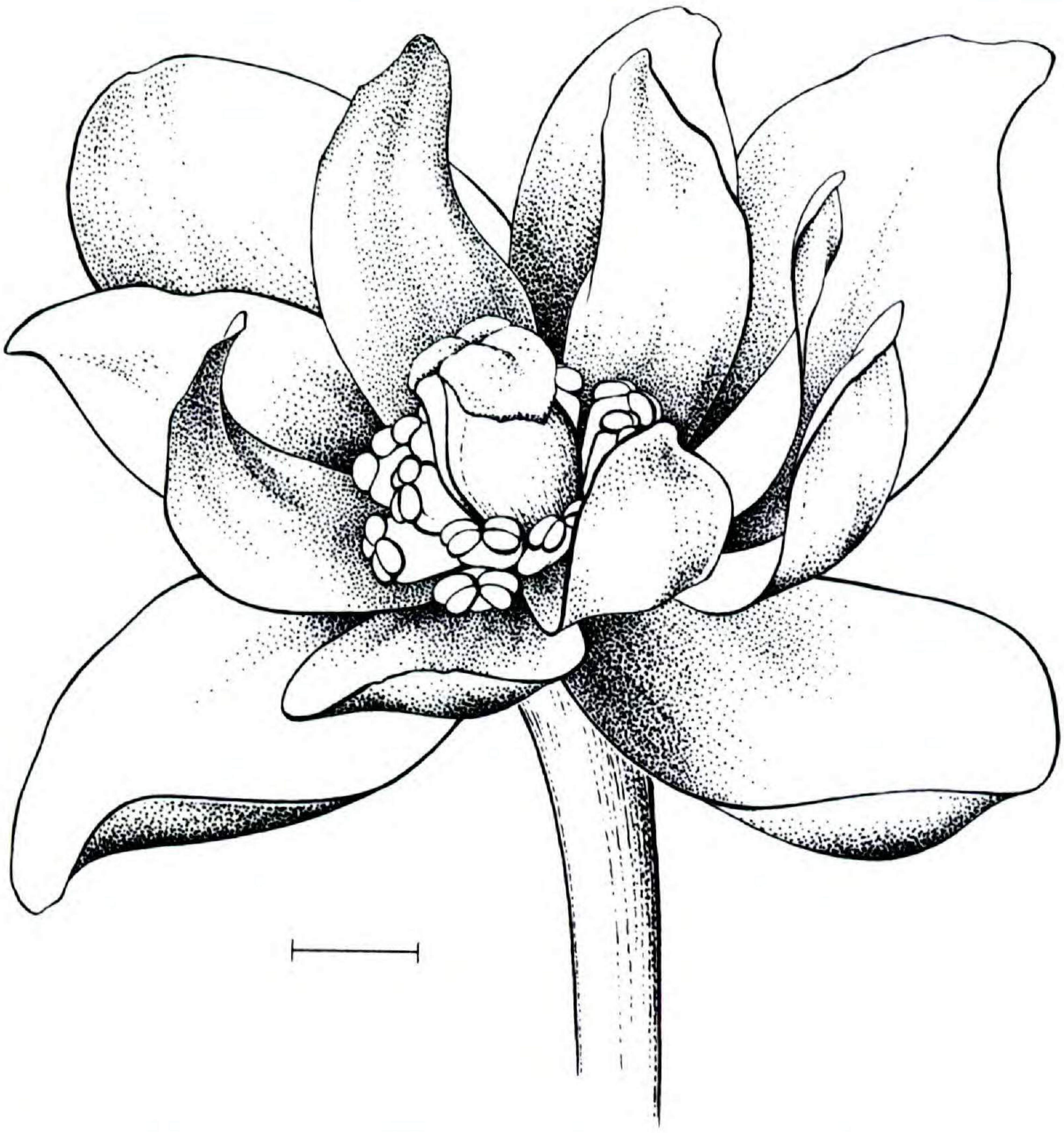

Figure 1. *Takhtajania perrieri.* Anthetic flower at female stage. Scale bar = 2 mm.

a more detailed description of the floral morphology and anatomy of *Takhtajania* and to compare it with that of other Winteraceae, especially the putatively basal *Tasmannia* and *Drimys.*

MATERIALS AND METHODS

Flowers fixed in FAA were used from the species and collections listed in Appendix 1.

Some of the flowers were embedded in Paraplast, sectioned with a rotary microtome at 10 μm, and stained with safranin and astrablue. Some of the flowers were embedded in Kulzer's Technovit 7100 (2-hydroxyethyl methacrylate), sectioned at 6 μm or less, and stained with ruthenium red and toluidine blue (for details of procedure, see Igersheim & Endress, 1997). For scanning electron microscope (SEM) studies, the specimens were dehydrated in ethanol and acetone and subsequently critical-point dried. The dried specimens were mounted on aluminium stubs and sputter-coated with gold. The confocal microscope photographs were taken by G. K. Rickards, School of Biological Sciences, Victoria University of Wellington, from a gynoecium (of a flower bud immediately before anthesis) cleared in 5% KOH at 40° for approximately 3 days and stained with ethydium bromide (1 microgram per ml).

Phylogenetic analysis was performed with PAUP* vers. 3.1.1, using the heuristic search option, algorithm TBR (tree bisection-reconnection branch swapping), and MULPARS (retention of all equally parsimonious trees) in effect. Consensus trees of shortest trees were gained by reweighting with a rescaled consistency index (CI) of original shortest trees.

RESULTS

ANTHETIC FLOWERS

The flowers of *Takhtajania* are ca. 1.5–2 cm across and have spreading red perianth parts at anthesis (Schatz et al., 1998) (Fig. 1). From the behavior of the stamens (see below) they are probably protogynous.

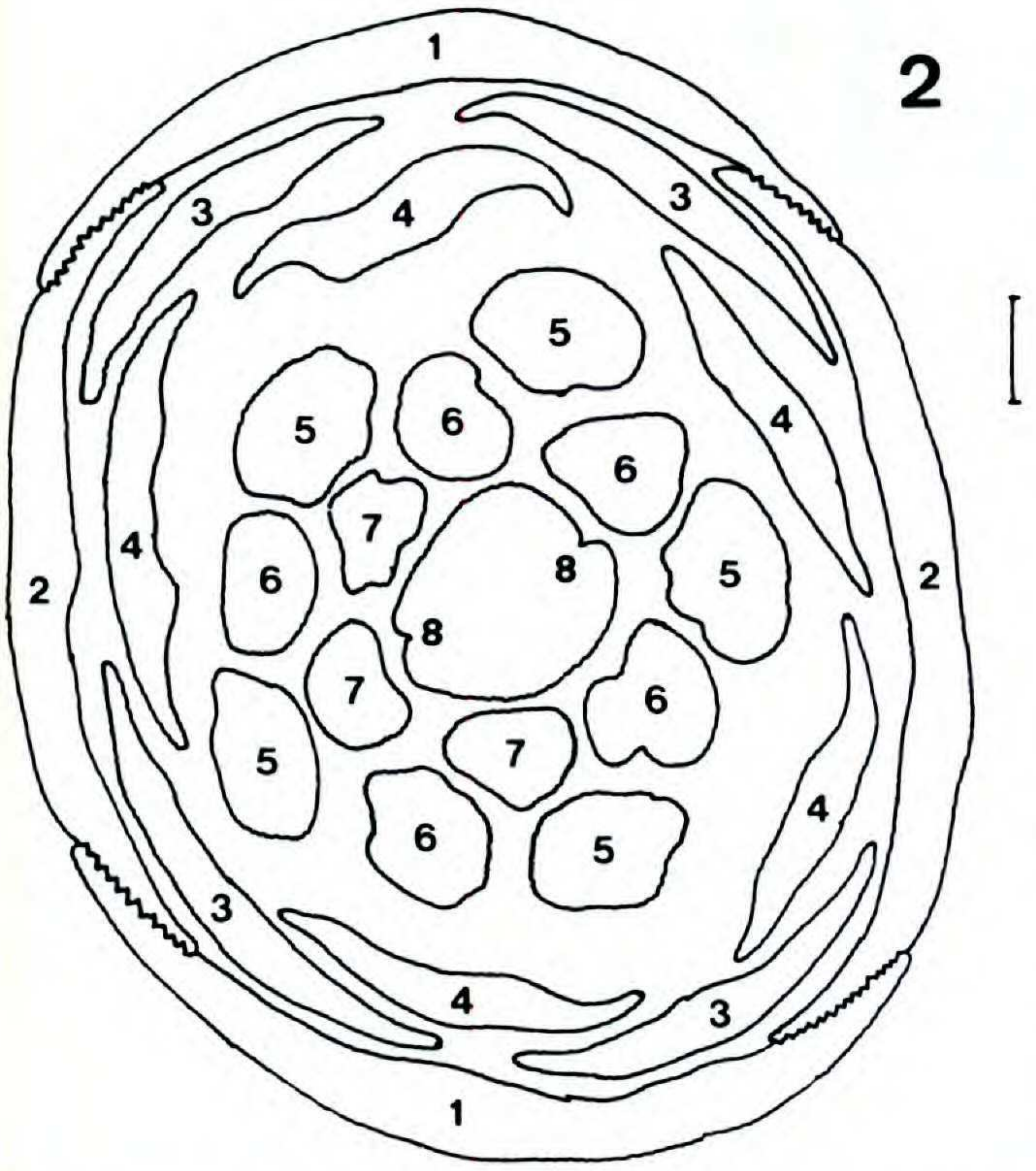

Figure 2. *Takhtajania perrieri.* Floral bud, transverse section; the numbers in the floral organs indicate whorls (1–4: tepals, 5–7: stamens, 8: carpels; the tepals of the involucre are not drawn, because they appear only in sections of the floral base; the tepals of whorl 1 and 2 are postgenitally fused in the overlapping area: marked by zigzag line; whorl 7 is one-sided). Scale bar = 0.5 mm.

NUMBER AND PHYLLOTAXIS OF FLORAL ORGANS

Floral phyllotaxis in Winteraceae is commonly irregular. There have been different attempts to derive phyllotaxis of particular groups from a spiral or whorled pattern (see discussion). In *Takhtajania* only scarce herbarium material has previously been studied, and it is not surprising that in each of the three publications that dealt with the arrangement of floral organs there is a different interpretation of floral phyllotaxis and merosity. These include: (1) outer six perianth parts decussate, stamens in three 4-merous whorls, one carpel (Capuron, 1963); (2) outer six perianth parts decussate, inner organs spiral, two carpels (Baranova & Leroy, in Leroy, 1978); (3) perianth parts in four 3-merous whorls, stamens in three whorls, the two outer ones 6-merous, the inner one 4-merous, two carpels (Vink, 1978).

We studied transverse microtome sections of eight floral buds close to anthesis to determine phyllotaxis and organ number; an example is illustrated in Figure 2. Organ position is somewhat unstable. However, there is a more or less whorled pattern with changing merosity from the outside to the center of the flower. The outermost floral organs are in dimerous alternating whorls. Then there is a switch to 4-merous alternating whorls. The result is that after a 2-merous whorl there appear two instead of one organ in each alternating position, and thus there are double positions instead of single positions (for discussion of double organ positions in flowers, see Endress, 1987, 1996). Then there is a further switch to 5-merous whorls by an additional double position. The innermost whorl of stamens may be incomplete on one side because of the asymmetric shape of the floral apex.

These switches in merosity do not always take place at the same site. All eight flowers studied begin with three 2-merous alternating whorls of tepals, followed by a 4-merous whorl of tepals (by double positions on the broader sides). In most flowers, the next whorl of tepals is 5-merous. Then two 5-merous whorls of stamens follow. The third whorl of stamens is either also 5-merous or there are only three (Fig. 2) or two stamens on one side of the flower (because the floral apex is slightly asymmetric). The gynoecium is 2-merous. In two of the flowers studied the transition to 5-mery was only in the second whorl of the androecium. One flower had two and one had three 4-merous whorls of tepals, and in both of them the first whorl of stamens was also 4-merous.

Thus the number of floral organs in the eight floral buds studied was: tepals (14–)15(–18), stamens 12–16, carpels 2. The previous counts by Capuron (1963), Baranova and Leroy (in Leroy, 1978), and Vink (1978) are all in this range, except that Vink found only 12 perianth parts.

PERIANTH

Winteraceae commonly have 2 (rarely 3) outer perianth organs that are more or less congenitally united and form a tight cover over the floral bud, which is often called the involucre or calyptra (e.g., Vink, 1988). The other perianth organs are free or more rarely some outer ones are (always postgenitally?) united. Terminology of the perianth organs of Winteraceae is not uniform in the previous literature. The involucre or calyptra was variously interpreted to be made up of bracts or sepals. The other perianth organs were variously called tepals, sepals, or petals (e.g., Nast, 1944; Capuron, 1963; Baranova & Leroy in Leroy, 1978; Vink, 1978; Gottsberger et al., 1980). There is no clear distinction between sepals and petals either in Winteraceae or in other basal angiosperms. Therefore, we prefer to use the term tepals for all perianth organs including those of the involucre (Hiepko, 1965; Endress, 1996).

In *Takhtajania*, the outer two tepals are congenitally united to form an involucre. Since they are much shorter than the other tepals, they do not protect the inner organs in older buds. Already in bud they form a more or less horizontal platform, which is somewhat elongated in the plane of its two tepals. The next inner four tepals (two pairs) form the topographical periphery of old floral buds. The outer two slightly overlap the inner two. In the overlapping region they are postgenitally united for about half of their length by interdentation of the cuticle (Figs. 2, 4A, B). As the flower opens this bond ruptures, and these four tepals are the first to spread. On their outer surface these four tepals are smooth and have a thick cuticle; on their inner surface they are papillate. All the following tepals have papillate surfaces. This papillate epidermis is tanniferous, as are the one or two cell layers below the epidermis. The margins of these tepals are not tanniferous; the cells are less vacuolate and have relatively large nuclei (Fig. 4C). From their appearance they seem to be secretory, and in microtome sections blue-staining secreted material is often concentrated around the tepal margins. This secretion was also observed in the field in June 1998 by G. Schatz. In the colored photographs of an open flower in Schatz et al. (1998) and in Schatz (2000 this issue), the red petals have white margins that correspond to this secretory zone. The material investigated contained insect (thrips?) larvae in the flower buds. It is uncertain whether these insects caused some of the secretion. Intercellular spaces in the tepals are not extensive. Starch is present especially around the vascular bundles.

The inner tepals commonly have three vascular bundles at their base, whereas the outer tepals have more. However, there is only one vascular strand from each tepal joining the stele in the floral base.

ANDROECIUM

At anthesis the stamens have apical extrorse anthers on club-shaped filaments (broadest shortly below the anther). Thus the thecae are basally spreading and almost horizontal. At the transition from the female to the male phase of anthesis, the filaments elongate and considerably thicken in the upper part, while the anthers shrink as they open (Fig. 5). As a result, the proportions of the stamens change considerably during anthesis. The filaments are more or less circular or slightly broader than thick in transverse section. The epidermis is slightly papillate and more or less tanniferous. Tanniferous tissue also occurs in scattered patches below the epidermis but is largely lacking in the center of the filament. This tanniferous region extends up to the ventral surface of the anther connective. Oil cells are present. Cells with oxalate crystals are lacking. The stamens contain a single collateral vascular bundle. The tissue around the vascular bundle contains abundant starch before the filament expands. After expansion the starch has disappeared (Fig. 6). Expansion of the filament goes hand in hand with cell enlargement.

GYNOECIUM

The gynoecium is disymmetric and club-shaped (Fig. 7D, E). It consists of two congenitally united carpels (Leroy, 1977; Vink, 1978). In young floral buds the tips of the two carpels can clearly be distinguished (Fig. 8A, B). At anthesis each carpel has a longitudinal furrow on its dorsal side (Fig. 7A, D). There are stomata on the outer surface (Fig. 7F). The gynoecium has a single locule. In the terminology of Leinfellner (1950) the entire ovary is symplicate; there is no synascidiate part at the base. The inner surface of the gynoecium is secluded from the outside by a completely postgenitally fused slit, which at the surface extends as a line between the two carpels (Figs. 3A, 9B). In the middle this line is crossed by a more or less distinct transverse furrow (Fig. 7B). The entire slit is surrounded by the stigma, which forms a large convex cap atop the gynoecium. The stigmatic zone is more extended in the commissural region than in the median plane of the carpels (Fig. 7D, E). The broadest part of the gynoecium, the ovary, is slightly above mid-length. Above the ovary there is a massive part with the common pollen tube transmitting tract (Figs. 3A–D, 9A–E). Below the ovary is a relatively long solid base, the common stipe of the two carpels (Fig. 3I–K). Although the ovary is unilocular, the placentae of the two carpels are obliquely directed; they meet in the center of the locule (Fig. 7G). They form an arch, which is deepest in the middle (Fig. 9A).

Each carpel has a dorsal vascular bundle, which extends up to some distance above the locule, where it may branch (Figs. 3A, 7G). The branches end about halfway between the level of the placentae and the stigma. Each carpel also has two or more lateral bundles, which are sometimes separate from the floral base (Figs. 3D–K, 7G). They flank the placentae and serve the ovules. They are connected with the dorsal bundles outside of the placentae and may also show connections between each other (Figs. 3C, 9C). The dorsal bundles commonly have two xylem portions that are directed toward each other and two phloem portions directed away from each other, which gives the appearance of two bundles (Fig. 3D–K). However, they probably originate from a single bundle. The same dou-

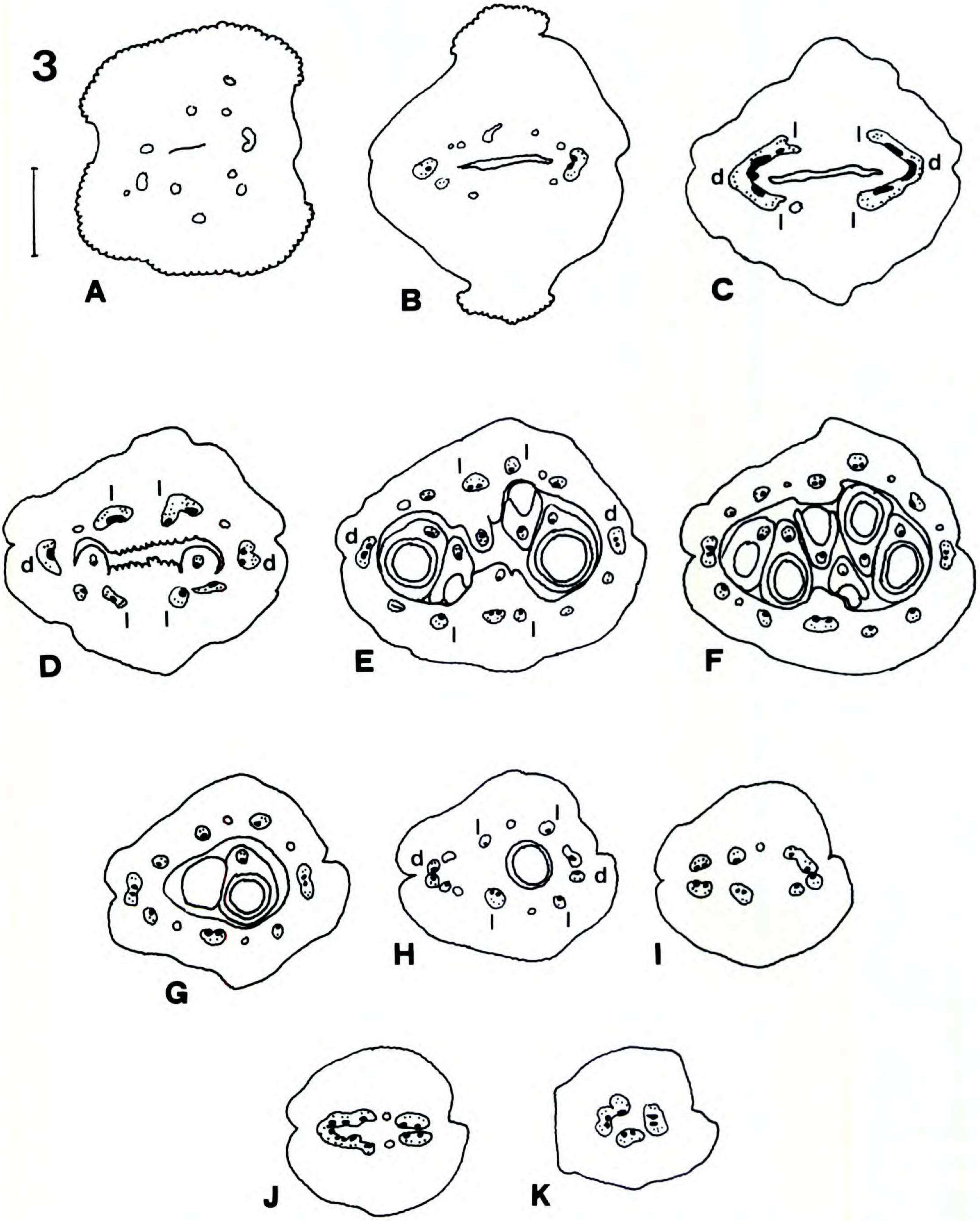

Figure 3. *Takhtajania perrieri.* Gynoecium at anthesis, transverse section series (d: dorsal vascular bundle, l: lateral vascular bundle). —A. Stigmatic zone, inner surfaces of gynoecium postgenitally fused. —B. Lowermost stigmatic zone, inner surfaces not fused. —C. Zone above ovary, lateral carpel vascular bundles merge with dorsal bundles. —D. Upper placental zone. —E. Lower placental zone. —F. Ovary with all ovules. —G, H. Ovary base. —I–K. Solid base of gynoecium with rearrangement of vascular bundles. Scale bar = 0.5 mm.

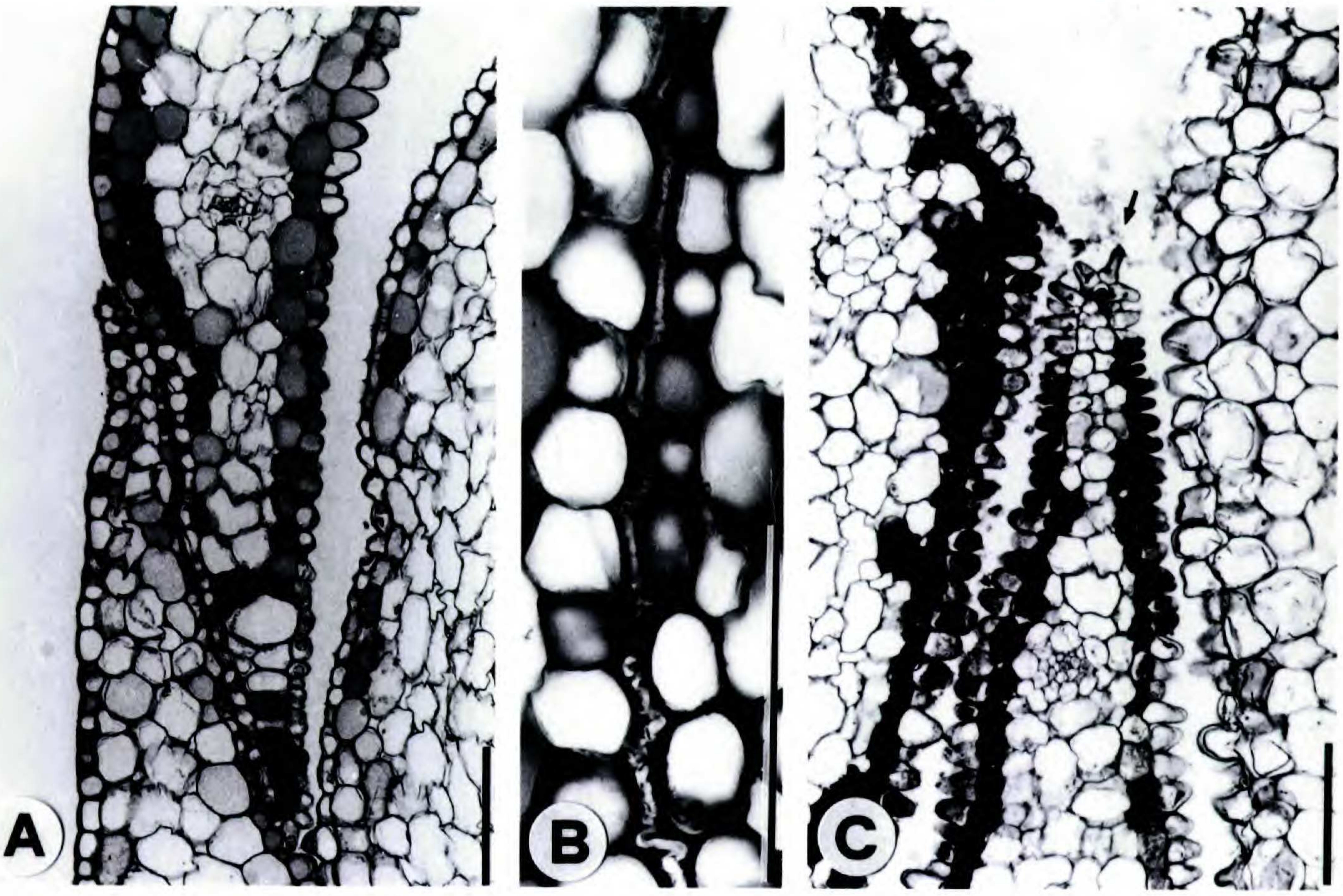

Figure 4. *Takhtajania perrieri.*—A. Transverse section of outer tepals in floral bud, showing postgenital fusion of overlapping area. —B. The same in higher magnification, showing interdigitation of cuticles of the postgenital fusion area. —C. Transverse section of non-tanniferous margin area of inner tepal, surrounded by secreted material (arrow). Scale bars in A and C = 0.1 mm, in B = 0.05 mm.

ble appearance also occurs in strong lateral bundles. Thus the ovules are served primarily by the lateral bundles, and not by the dorsal bundles (in contrast to the interpretation by Deroin & Leroy, 1993; see discussion) (Fig. 7G).

The stigmatic surface is unicellular-papillate and secretory (Fig. 7C). Also the pollen tube transmitting tissue that lines the inner gynoecium surface down to the placentae has large, unicellular papillae (Fig. 9E). The stigmatic papillae are tanniferous and the several cell layers of the tissue below them still more so (Fig. 9A, B). Below the region of the pollen tube transmitting tissue, the inner surface of the ovary is lined with about two layers of tanniferous cells. Throughout the gynoecium there are scattered tanniferous cell groups. The gynoecium wall also contains ethereal oil cells. Cells with oxalate crystals are present. The inner layers of the ovary wall contain abundant starch. Stomata are scattered over the surface of the gynoecium, especially in its upper part. Stone cells were not found in the gynoecium.

In 31 flowers studied we found (5–)6–7(–8) ovules per gynoecium (1 with 5, 9 with 6, 16 with 7, 5 with 8 ovules). Capuron (1963) and Leroy (1978) mentioned 5–11 ovules for the type material; however, in the figures by Vink (1978) and Deroin and Leroy (1993) there are only four ovules in a gynoecium. The ovules are pendent and are arranged in two lines. They are bitegmic, crassinucellar, and anatropous (Fig. 10). They are ca. 900 μm long. Ovule width/length ratio is 0.6. The nucellus is ca. 280 μm broad. The micropyle is formed by the inner integument (Fig. 10). The outer integument is semiannular, and the inner is annular (Fig. 10A, B). However, of the 31 gynoecia studied we found two in which one of the six ovules was orthotropous and both integuments were annular; the orthotropous ovule was smaller than the other ones and had a long funicle. In transverse section the ovules are wedge-shaped because they alternate on both sides of the double placenta and are wedged together (Figs. 3F, 9F). The outer integument is 4–5 cell layers thick, and the inner is 3 cell layers thick. Tanniferous tissue occurs mainly in the periphery of the ovule (outer integument and raphe, especially around the vascular bundle).

DISCUSSION

NUMBER AND PHYLLOTAXIS OF FLORAL ORGANS

Lability of floral organ number and phyllotaxis, and the tendency toward some irregularity and

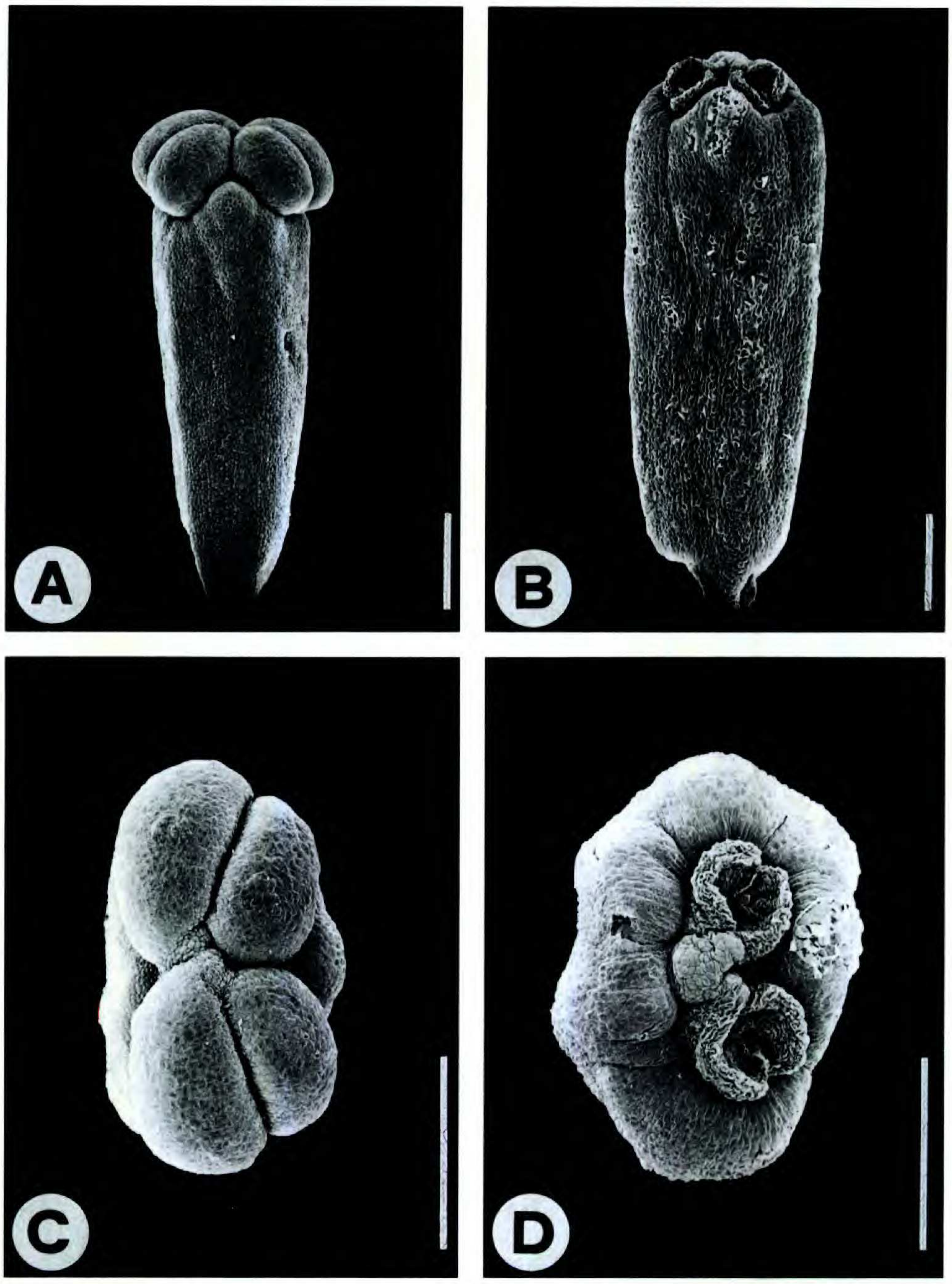

Figure 5. *Takhtajania perrieri.* Inner stamen in female and male phase of anthesis; in the male phase the filament is inflated and the anthers are open and shrunken; each pair of figures is at the same magnification. A, B. From dorsal side. —A. Female phase. —B. Male phase. C, D. From above. —C. Female phase. —D. Male phase. Scale bars = 0.5 mm.

asymmetry, is common in flowers of Winteraceae and is also present in *Takhtajania.* Floral phyllotaxis seems to be predominantly irregularly whorled in Winteraceae (Vink, 1970, 1977, 1978, 1985, 1993b; Endress, 1986, 1987). From the record in the literature, *Drimys winteri* seems to be an interesting exception with more or less regular spiral floral phyllotaxis (Hiepko, 1966; Erbar & Leins, 1983). However, Ronse Decraene and Smets (1998) mentioned chaotic floral phyllotaxis also for *Drimys winteri.* Doust (1997) shed light on this seeming contradiction by his observation that terminal flowers in *Drimys winteri* have a more or less spiral pattern, while lateral flowers have more chaotic patterns due to initial asymmetries of the floral apex (see also Vink, 1970); Doust (1997) also found that terminal flowers have more floral organs than lateral ones.

Notwithstanding this irregularity, there is a most common pattern within the family: The outer floral organs are decussate. Then there is a change to 4-merous alternating whorls and sometimes, by additional double positions, to whorls with a higher number of organs. This was reported to be common for *Pseudowintera* (less common in *Tasmannia*) (Vink, 1970), and for *Zygogynum* (Vink, 1977, 1983, 1988). As shown here, it is also present in *Takhtajania.*

PERIANTH

In *Takhtajania* the two outermost, congenitally united tepals, which form the involucre, are much

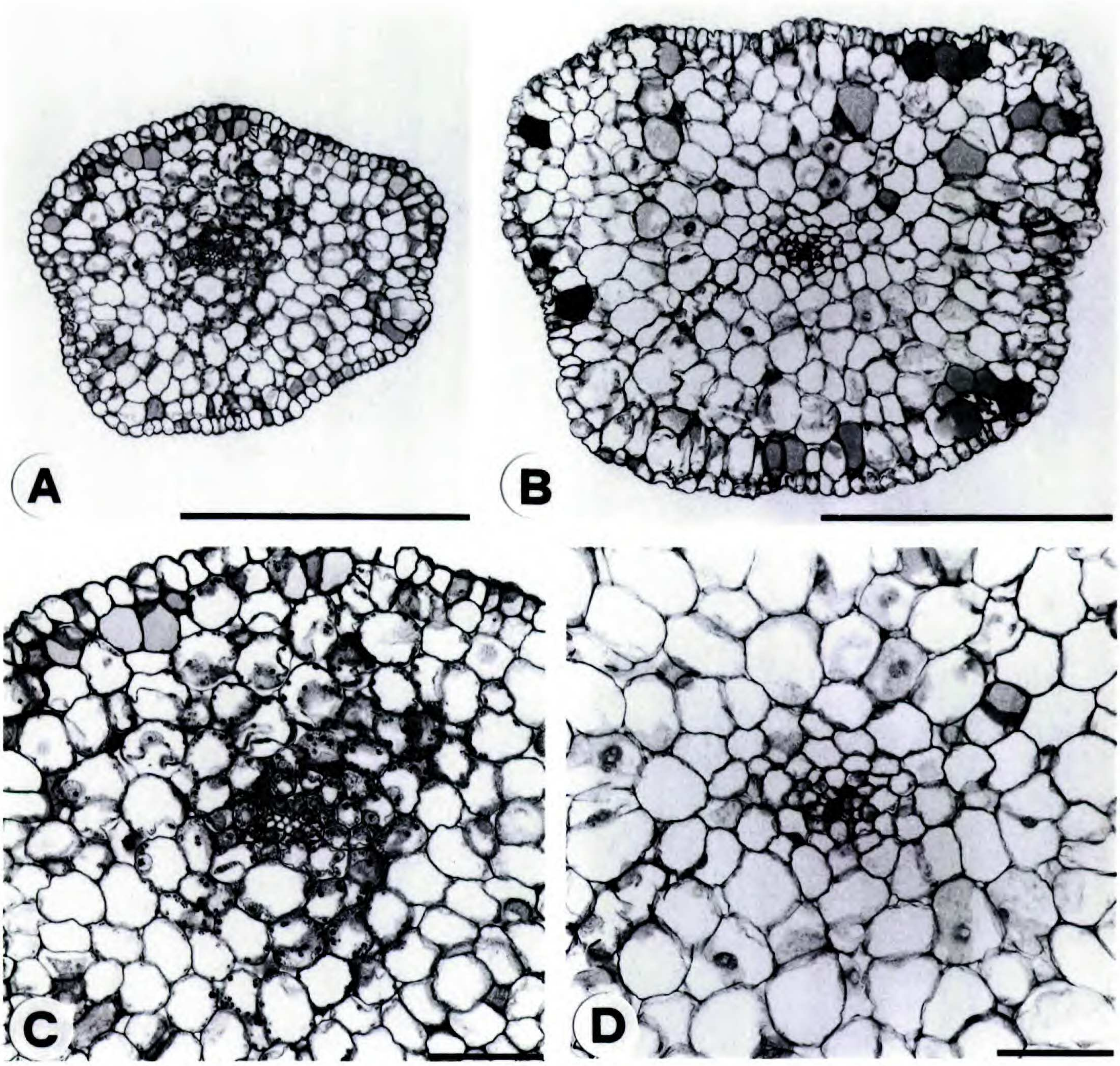

Figure 6. *Takhtajania perrieri.* Transverse sections of filaments of inner stamens immediately below anthers, in female and male phase of anthesis; in the male phase the filament is inflated by cell enlargement, and starch, which was present in the female phase, has disappeared; each pair of figures is at the same magnification. A, B. Entire transverse section. —A. Female phase. —B. Male phase. C, D. Central part of A and B at higher magnification. —C. Female phase (note starch grains in tissue around vascular bundle: dark dots). —D. Male phase (starch grains no longer present). Scale bars in A and B = 0.5 mm, in C and D = 0.1 mm.

shorter than in *Drimys* and *Tasmannia,* where they are protective organs for the buds. In *Drimys* and *Tasmannia* the involucre encloses the other floral parts until the flower opens, while in *Zygogynum* and *Pseudowintera* it ruptures very early and the next inner tepals attain a protective function (Vink, 1988). The next inner whorl of tepals is postgenitally united in *Takhtajania.* Such union is also reported for some *Zygogynum* species but not for other Winteraceae (Vink, 1985, 1988; although without indication whether it is postgenital or congenital). We did not find tepals with secretory margins in *Drimys* and *Tasmannia.* In addition, the epidermis was tanniferous and not papillate in those genera. Tepals are white in *Drimys* and *Tasmannia* because of large intercellular spaces in the mesophyll, which form an optical tapetum that reflects incoming light. *Takhtajania,* in contrast, without an optical tapetum, has red tepals, as do some species of *Zygogynum,* but those have much thicker tepals (see Thien, 1980; Vink, 1993a). In addition to *Takhtajania,* some other Winteraceae contain starch in the tepals, which, at least in some, may provide food for pollinators (beetles, thrips) (Pellmyr et al., 1990; Thien et al., 1990).

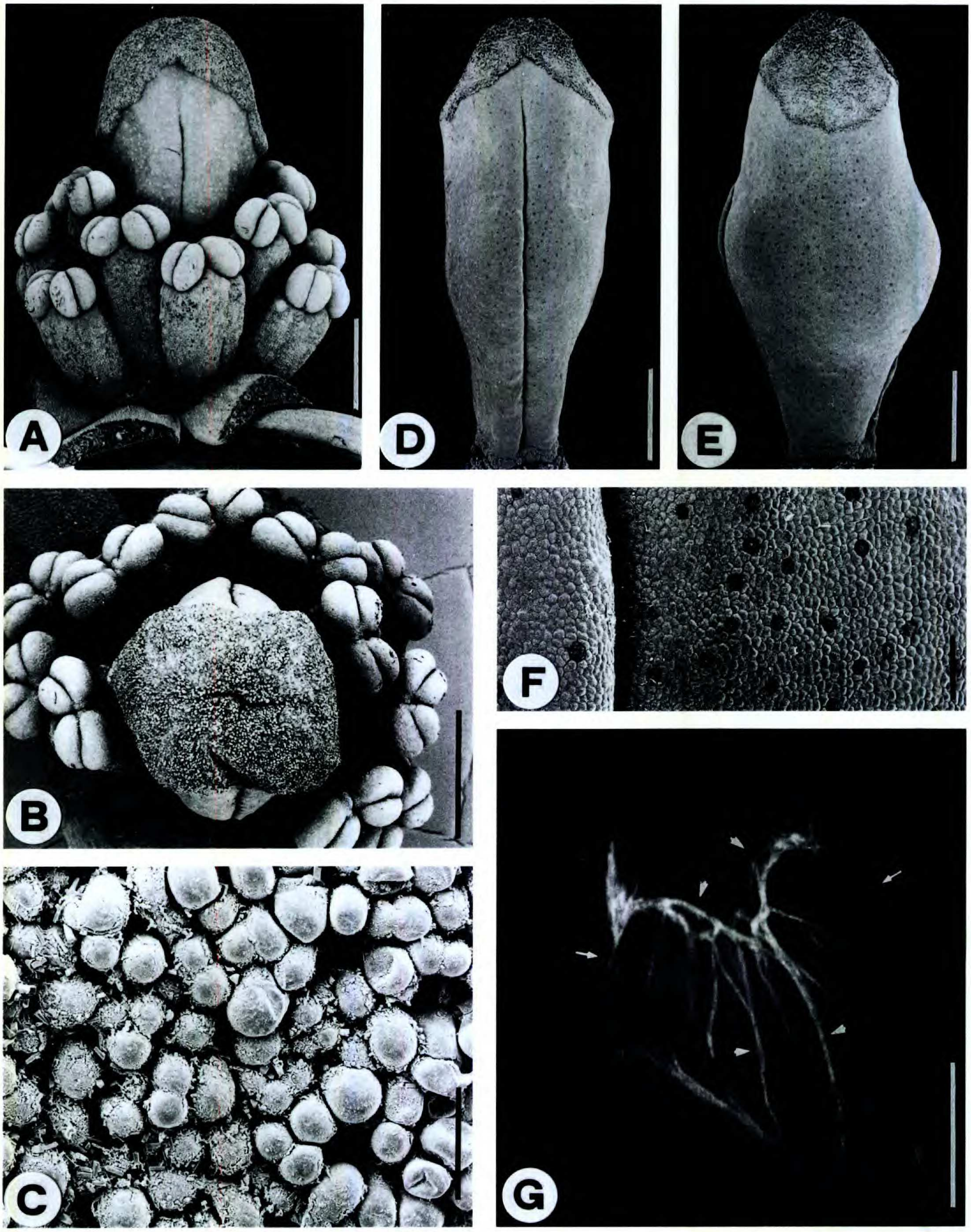

Figure 7. *Takhtajania perrieri.* A–C. Flower in female phase of anthesis. —A. Flower from the side, tepals broken off. —B. From above. —C. Stigmatic papillae with secretion. D–F. Gynoecium, from the side, shortly after anthesis. —D. Showing dorsal side of one of the two carpels, with longitudinal furrow. —E. Gynoecium rotated at 90°. —F. Magnification of D, showing stomata on gynoecium surface. —G. Confocal laser photograph showing vasculature (xylem) of a gynoecium (same view as E), arrows = dorsal vascular bundles, arrow-heads = lateral vascular bundles. Scale bars in A, B, D, E, and G = 1 mm, in C = 0.05 mm, and in F = 0.1 mm.

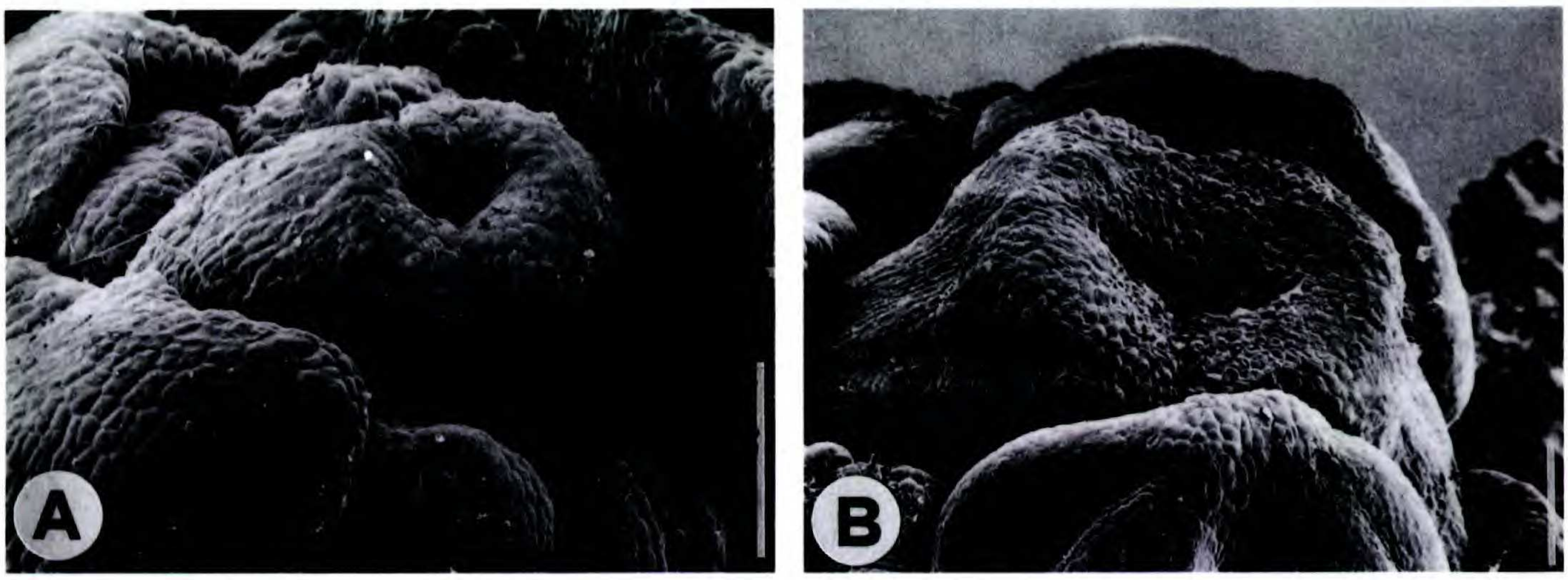

Figure 8. *Takhtajania perrieri.* Gynoecia of young floral buds, from the side. —A. Before beginning of stigma formation. —B. At beginning of stigma formation. Scale bars = 0.1 mm.

ANDROECIUM

Club-shaped filaments with the thecae on top as in *Takhtajania* also occur in *Pseudowintera* and *Zygogynum.* In *Drimys* and even more so in *Tasmannia* the filaments are thinner and the thecae are less terminal and more lateral (Bailey & Nast, 1943a; Sampson, 1987; Endress & Hufford, 1989; Endress, 1994).

The behavior of the stamens of *Takhtajania* during anthesis with elongation and especially thickening and broadening of the filament is also characteristic for other Winteraceae. It was shown for *Pseudowintera* by Sampson (1980) and Lloyd and Wells (1992), and for *Zygogynum mackeei* Vink, *Z. stipitatum,* and *Z. pancheri* by Carlquist (1981, 1982, 1983). Carlquist (1982) also noted the decrease in starch content in stamens of *Z. stipitatum.* He discussed filament expansion in the context of flower opening by pressure of the stamens. However, we found the conspicuous filament expansion only after flower opening, at the transition from the female to the male phase and interpret it as associated with pollen presentation (see also Sampson, 1980, for *Pseudowintera*). Loss of starch may be correlated with rapid cell growth in this phase, as also indicated by Carlquist (1982) for *Zygogynum stipitatum.* It should also be studied whether starch loss is here associated with scent production, as this often occurs in osmophores (Vogel 1990). Pellmyr et al. (1990) discussed the significance of floral scents in Winteraceae for pollination but did not mention the source of the scents (see also section on perianth).

Since the thecae in *Takhtajania* are on top of the club-shaped filaments, the position of the thecae is highly oblique to almost horizontal (also in *Pseudowintera* and *Zygogynum*). Therefore, in transverse sections of stamens the thecae are cut obliquely. As a consequence, the endothecium, which is one-layered, may appear to be two- or more-layered (see Swamy, 1952, for *Zygogynum baillonii*), while in reality it is only one-layered.

GYNOECIUM

The gynoecium of *Takhtajania* is peculiar. Although it is bicarpellate and unilocular, it is not paracarpous in the normal sense with parietal placentation. The placentae are not vertical but oblique to almost horizontal. Therefore, the placentae of both carpels are separate and are only contiguous at their morphological bases. Thus, placentation is not laminar (as opposed to Leroy, 1993) but has a normal linear configuration. The stigma is topographically apical, but morphologically it surrounds the entire (postgenitally fused) entrance into the internal space of the two carpels. The stigma is not commissural either (as opposed to Leroy, 1980, 1993), because the entire orifice is stigmatic and not only the lateral parts, although the stigmatic surface is more extended in the commissural than in the median region. Thus, it corresponds to the stigma extension of most other Winteraceae, which have a double-crested stigma with the crests confluent at both ends.

This unique bicarpellate unilocular gynoecium of *Takhtajania* could have evolved from a unicarpellate ancestor. Unicarpellate gynoecia are known from species of *Tasmannia, Pseudowintera,* and *Zygogynum* (*Bubbia*) (Sampson, 1963; Vink, 1970, 1983, 1993a; Ueda, 1986). In these species, sometimes two carpels instead of one carpel develop in a flower (Sampson & Kaplan, 1970). In such gynoecia, the available space for two carpels is limited so that they may form a unilocular paracarpous structure, as Sampson and Kaplan (1970) showed for *Pseudowintera traversii* Dandy. Furthermore, in

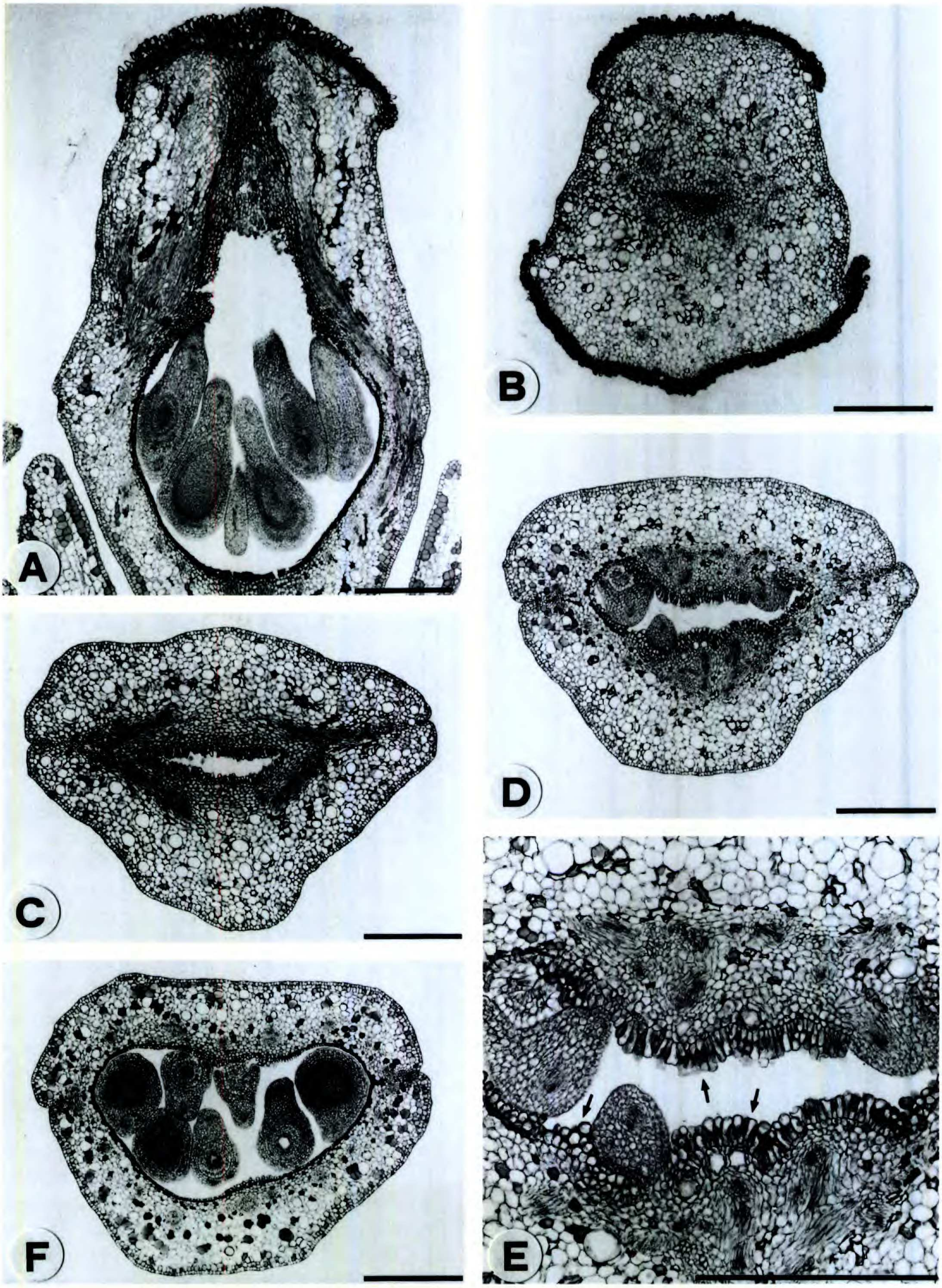

Figure 9. *Takhtajania perrieri.* —A. Gynoecium at anthesis, in approximately median longitudinal section. B–F. Gynoecium at anthesis, transverse section series. —B. Stigmatic zone, inner surfaces of gynoecium postgenitally fused. —C. Zone above placenta, inner surface not fused. —D. Upper zone of placenta. —E. Same in higher magnification, showing the papillate pollen tube transmitting tissue (arrows). —F. Ovary, showing the transversely sectioned wedge-shaped ovules. Scale bars = 0.5 mm.

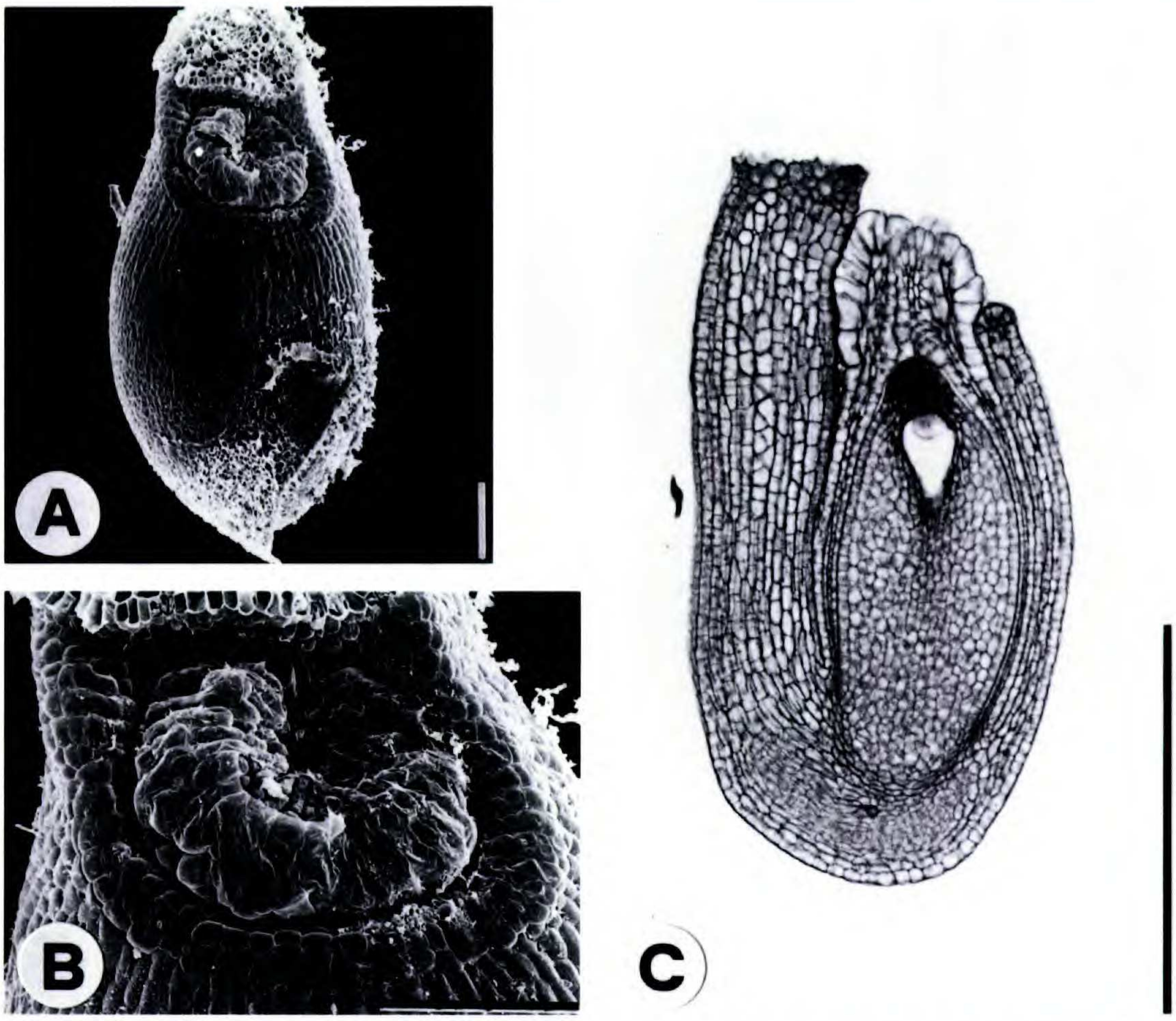

Figure 10. *Takhtajania perrieri.* Ovules at anthesis. —A. Ovule from micropylar side, micropyle formed by the inner integument (arrow), outer integument semiannular. —B. Same, micropylar part in higher magnification. —C. Ovule in approximately median longitudinal section. Scale bars in A and B = 0.1 mm, in C = 0.5 mm.

Zygogynum two (or three?) central stigmas of a gynoecium may be confluent (*Z. baillonii,* Vink, 1993a). A dorsal furrow in the carpels as in *Takhtajania* also occurs in *Tasmannia lanceolata* (Leinfellner, 1965; Vink, 1970; Leroy, 1980). The position of the furrows is dorsal because they alternate with the two placentae in the bicarpellate, syncarpous gynoecium of *Takhtajania.* In the free carpels of *Tasmannia,* the furrow lies opposite the placenta. The significance of the furrows is not clear; dehiscence of the mature fruits has not been reported. Another, more conventional hypothesis is evolution of the gynoecium of *Takhtajania* from two free carpels.

In their discussion, Deroin and Leroy (1993) mentioned the apical placenta of *Takhtajania* as peculiar. This differs from the gynoecium in paracarpous Annonaceae, with which they made a comparison. However, it is not peculiar within Winteraceae, because the majority of them have "apical" placentae (because of their more or less horizontal direction).

How does the gynoecium of *Takhtajania* compare with that in other Winteraceae (apart from its peculiar syncarpy)? Several authors published studies on more than one genus of the Winteraceae that may serve as a comparative basis for this question: (1) the studies by Bailey and Nast (1943b, 1945) and Bailey and Swamy (1951) especially focused on the vasculature; (2) the studies by Tucker (1959, 1975), Tucker and Gifford (1964, 1966a, b), Sampson (1963), Sampson and Kaplan (1970), and Sampson and Tucker (1978) concentrated on the morphological and anatomical development of carpels, vascularization, and placentation; (3) the studies by Leinfellner (1965, 1966a, b, 1969) primarily dealt with the outer and inner morphology and placentation; (4) the study by Igersheim and Endress (1997) focused on morphology and histology of carpels and ovules in comparison with that in other Magnoliales and winteroids.

Leinfellner (1965, 1966a, b, 1969) and Tucker and Gifford (1966b) found an unusually high variability of carpel shapes in Winteraceae from highly ascidiate to largely plicate. Non-ascidiate carpels as in *Takhtajania* are only known from *Tasmannia* (see also Frame, 1996). However, these are not directly comparable, because the non-ascidiate shape in *Takhtajania* may be caused by its syncarpy, while *Tasmannia* is apocarpous.

Gynoecium vasculature of *Takhtajania* is not different from that in other Winteraceae. The ovules are served primarily by lateral bundles (see also Vink, 1978), and not predominantly by the dorsal bundles as contended by Deroin and Leroy (1993). Carpels in Winteraceae generally have a dorsal vascular bundle, which has sometimes been characterized as "double," or there are two dorsal bundles, such as in *Tasmannia* (Tucker & Gifford, 1964); in addition, there are two ventral (lateral) bundles associated with the placentae, which may merge into one bundle in the ascidiate basal part of the carpel. Dorsal and lateral vascular bundles may be connected by secondary bundles later in development. In a critical study Tucker (1975) showed that ovules are principally served by lateral carpellary vascular bundles in species of *Drimys* and *Tasmannia*. In contrast, Bailey and Nast (1943b) had described the ovules as being vascularized partly by branches of the dorsal strands, and partly by anastomoses between dorsal and ventral strands. It seems to be a peculiarity that the ovular vascular strands differentiate relatively late, when the dorsal and ventral vascular bundles are already far differentiated. This is probably due to the fact that the ovules arise relatively late, when the carpels are already relatively massive and the primary vasculature is relatively advanced in development. As a consequence, the ovular traces connect with secondary vascular bundles between the lateral and dorsal main strands that have formed later. However, the connection with the lateral vascular bundles is still there (Tucker, 1975; see also Ueda, 1978). Likewise, in *Takhtajania*, the ovules are served by lateral vascular bundles or by connections between the dorsal and lateral ones (and not by dorsal ones as Deroin & Leroy, 1993, described).

The ovules of *Takhtajania* are much larger at anthesis than those in all other taxa of Winteraceae studied (see list in section "Material and Methods"). The ovules of *Takhtajania* are 900 μm long, whereas those of the other taxa investigated vary between 330 μm in *Tasmannia insipida* and 625 μm in *Zygogynum baillonii*. This may be correlated with the low number of ovules per ovary in *Takhtajania* and the different architecture of the bicarpellate unilocular ovary as compared to the ovary in free carpels. In morphology and histology (especially distribution of tannins), the ovules are similar to those of other Winteraceae (see Strasburger, 1905; Bhandari, 1963; Sampson, 1963; Bhandari & Venkataraman, 1968; de Boer & Bouman, 1974; Prakash et al., 1992; Imaichi et al., 1995; Igersheim & Endress, 1997; Svoma, 1998).

SYSTEMATICS OF WINTERACEAE AND SYSTEMATIC POSITION OF *TAKHTAJANIA*

Before recognition of *Takhtajania*, *Tasmannia* and *Drimys* were considered to be the basal branches in Winteraceae. *Tasmannia* was favored as the basalmost clade because of its low chromosome numbers (Ehrendorfer et al., 1968) and the conduplicate carpels (Smith, 1969) long viewed as a model for an archaic carpel form (Bailey & Swamy, 1951). *Drimys* was considered as the closest neighbor of *Tasmannia* because of many morphological similarities. In fact, for some time *Tasmannia* was subsumed under *Drimys*. However, chromosome studies by Ehrendorfer et al. (1968) prompted Smith (1969) to reinstate *Tasmannia*. The ITS studies by Suh et al. (1993) supported the split between the two genera. They also supported *Tasmannia* as sister of the rest of the family, which has *Drimys* in the basal position, followed by *Pseudowintera* and *Zygogynum* (the latter including *Bubbia*, *Belliolum*, and *Exospermum*, as proposed by Vink (1985) on morphological grounds; see also Vink, 1993b). Kubitzki and Reznik (1967) found a persistent difference in leaf flavonoids between *Drimys* and *Tasmannia*. The isolated position of *Tasmannia*, as well as the unity of the group *Bubbia*, *Belliolum*, *Exospermum*, and *Zygogynum*, was emphasized by Williams and Harvey (1982) based on the leaf flavonoid patterns. However, they interpreted *Tasmannia* as the most advanced genus in the family. On the basis of leaf epidermis, Baranova (1972) considered the basal dichotomy to be between *Drimys/Tasmannia* and *Bubbia/Belliolum/Pseudowintera/Zygogynum*; further, she emphasized the isolated position of *Bubbia perrieri*.

After *Takhtajania* was recognized as a separate genus, Vink (1988) explicitly proposed a basal position in the family for it, followed by a *Tasmannia/Drimys* clade. A basal position of *Takhtajania* had also been implied by Leroy (1978) by the erection of a subfamily Takhtajanioideae and later even a separate family Takhtajaniaceae (Leroy, 1980). Family status was later not accepted by other authors and was also rejected by Leroy (1993). Even before *Takhtajania* was erected as a genus and was still included in *Bubbia* as *B. perrieri*, Bongers (1973) found that alveolar material was present on the leaf surface of Winteraceae except for *Tasmannia* and *Bubbia perrieri*. In contrast, in view of its very large pollen tetrads and its particular pollen structure (Lobreau-Callen, 1977), which may indicate polyploidy, *Bubbia perrieri* was considered to be related to *Belliolum* (*Zygogynum*) and *Drimys* rather than *Tasmannia* (for correlation of chromo-

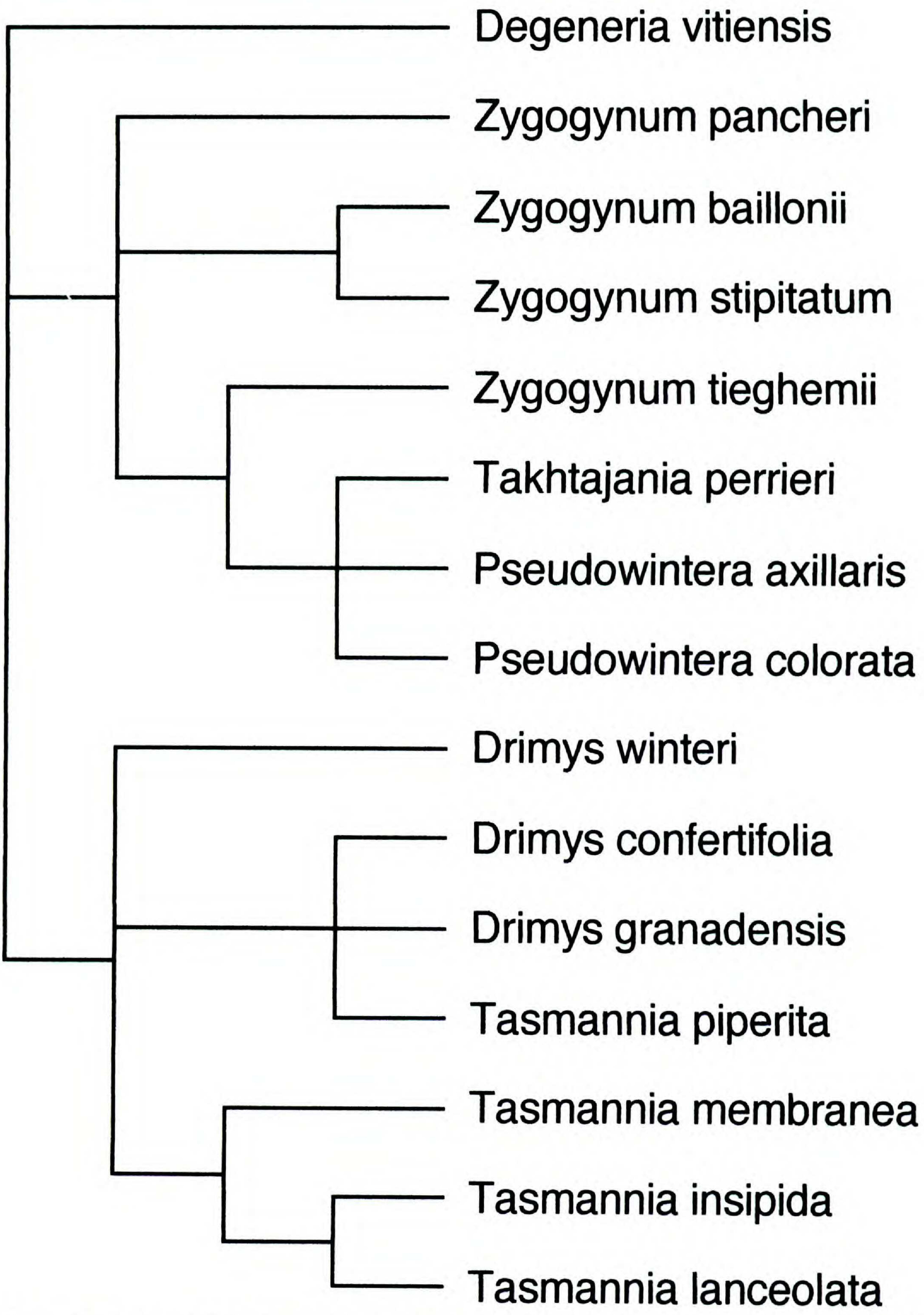

Figure 11. Cladogram of the representatives of Winteraceae studied, with *Degeneria* as outgroup, based on 13 representative floral features, showing *Takhtajania* nested in the *Pseudowintera/Zygogynum* clade (PAUP 3.1.1, heuristic search, TBR: consensus tree of 3 shortest trees with CI 0.765, RI 0.894, gained by reweighting with rescaled CI of 25 shortest trees of length 29 with CI 0.621 and RI 0.788).

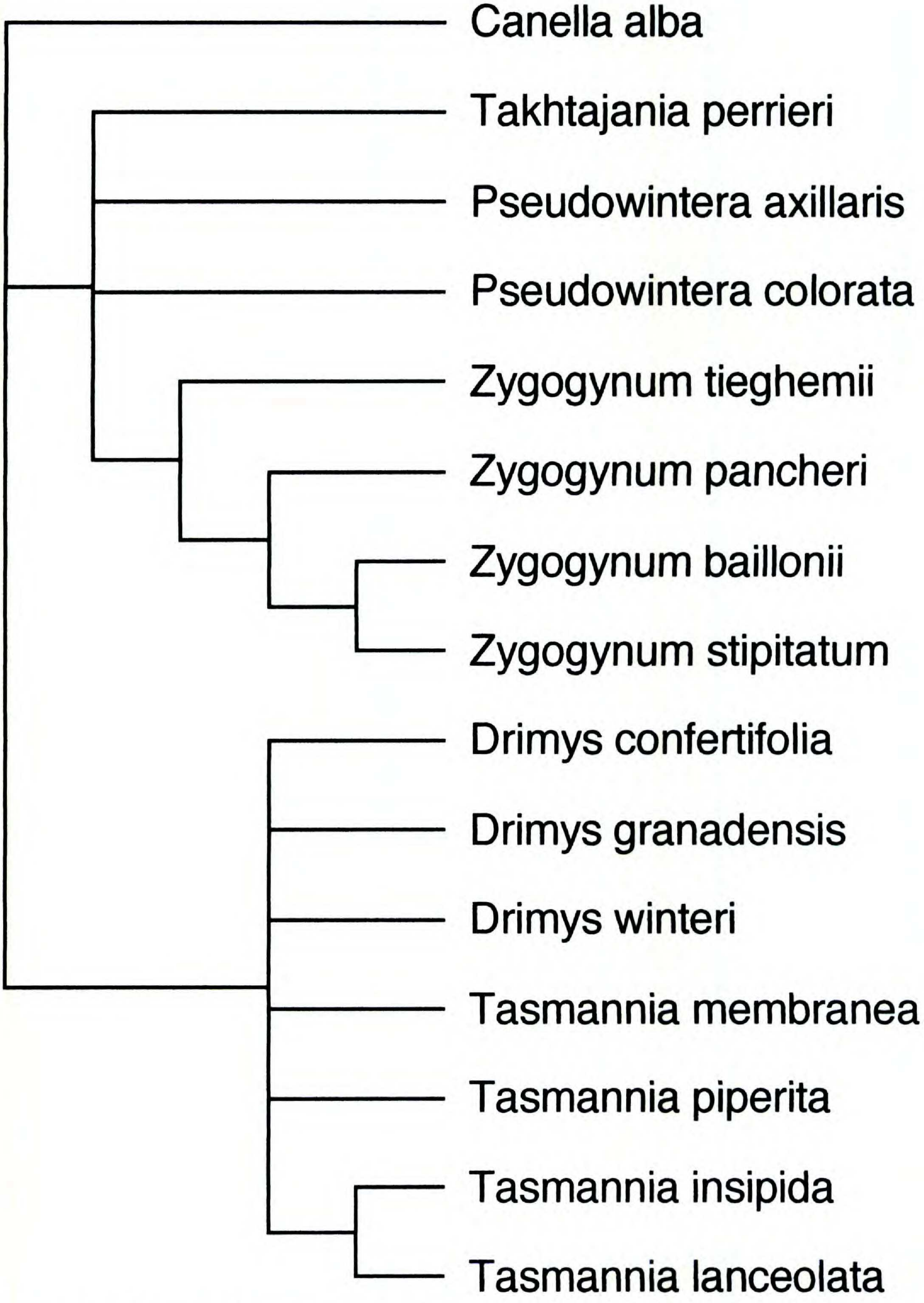

Figure 12. Cladogram of the representatives of Winteraceae studied, with *Canella* as outgroup, based on 13 representative floral features, showing *Takhtajania* nested in the *Pseudowintera/Zygogynum* clade (PAUP 3.1.1, heuristic search, TBR: consensus tree of 20 shortest trees with CI 0.713, RI 0.868, gained by reweighting with rescaled CI of 70 shortest trees of length 30 with CI 0.600 and RI 0.769).

some number and pollen size in Winteraceae, see Hotchkiss, 1955). Praglowski (1979) emphasized the special similarity of its pollen tetrads with those of *Drimys*.

From the results of the present comparative study of flowers of *Takhtajania* and other Winteraceae some new features come into the discussion. The particular club-shaped stamens and almost horizontal position of the thecae are shared with *Pseudowintera* and *Zygogynum*. The presence of an involucre that is short and protective only in young floral buds is shared with *Pseudowintera* and *Zygogynum*. The presence of whorls of 4 or 5 tepals is shared with *Pseudowintera* and *Zygogynum* species. The fusion of the tepals following the involucre is shared with some *Zygogynum* species. Red tepal color is shared with some *Zygogynum* species. This and the large pollen grains may indicate that *Takhtajania* constitutes a clade with the *Pseudowintera/Zygogynum* group and that a *Tasmannia/Drimys* group is sister to this clade (see also fig. 2.2 in Vink, 1988). This is also shown by a cladogram based on representative floral characters (Fig. 11; Appendixes 2, 3) and with *Degeneria* as an outgroup, a genus that tends to come out as sister group of Winteraceae in preliminary cladistic analyses based on gynoecium structures through all families of the basal angiosperms.

Another scenario, indicated by molecular data (Karol et al., 2000 this issue) shows a sister relationship of Winteraceae and Canellaceae. But even with Canellaceae as an outgroup, *Takhtajania* appears nested in a *Pseudowintera/Zygogynum* clade in the morphological analysis (Fig. 12; Appendixes 2, 3). If this scenario with Canellaceae sister to Winteraceae stands corroborated, the alternative view with *Takhtajania* basal in Winteraceae would be better supported. *Takhtajania* shares with Canellaceae having red flowers with whorled phyllotaxis and only a short involucre of united outer tepals. They also share a bicarpellate, paracarpous gynoecium, which, however, is different in detail. Canellaceae have vertical parietal placentae and campylotropous ovules with zig-zag micropyle, but *Takhtajania* has obliquely horizontal separate placentae that meet at their morphological base, and anatropous ovules with micropyle formed by the inner integument; see Igersheim & Endress (1997). Thus the paracarpous gynoecium is unlikely to be a synapomorphy for *Takhtajania* and Canellaceae. In addition to molecular studies, the karyotype of *Takhtajania* will be crucial in a phylogenetic interpretation.

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Appendix 1. Preserved (FAA) specimens examined (specimens are housed at Z).

Drimys confertifolia Phil. Chile. Juan Fernandez Islands, Masatierra, *T. F. Stuessy et al. 5474.*

Drimys granadensis L.f. Costa Rica. Volcan Poas, *P. K. Endress 97-127.*

Drimys winteri J. R. & G. Forst. Switzerland. Cult. Isole di Brissago, *P. K. Endress 6524.*

Pseudowintera axillaris (J. R. & G. Forst.) Dandy. New Zealand, *P. K. Endress 6357.*

Pseudowintera colorata (Raoul) Dandy. Germany. Cult. Botanic Garden, University of Bonn, *P. K. Endress 4552.*

Takhtajania perrieri (Capuron) Baranova & J.-F. Leroy. Madagascar. Anjahanaribe-Sud RS., *P. J. Rakotomalaza et al. 1342, 13 VI 1997*; *G. E. Schatz 3748, VI 1998* (Fig. 1); *D. Ravelonarivo s.n., III 1998* (Fig. 8).

Tasmannia insipida R.Br. ex DC. Australia. Southern Queensland, *P. K. Endress 4294.*

Tasmannia lanceolata (Poir.) A. C. Sm. New Zealand. Cult. Botanical Garden, University of Canterbury, Christchurch, *D. G. Lloyd, s.n.*, 23 IX 1992.

Tasmannia membranea (F. Muell.) A. C. Sm. Australia. Northern Queensland, *P. K. Endress 4215.*

Tasmannia piperita (Hook. f.) A. C. Sm. Papua New Guinea, *P. K. Endress 4137.*

Zygogynum baillonii Tiegh. New Caledonia, *P. K. Endress 6295.*

Zygogynum pancheri (Baill.) Vink. New Caledonia, *P. K. Endress 6251.*

Zygogynum stipitatum Baill. New Caledonia, *A. M. Juncosa s.n.*, 1981.

Zygogynum tieghemii Vink. New Caledonia, *P. K. Endress 6329.*

Appendix 2. Matrix of 13 representative floral characters of *Takhtajania perrieri* and 13 other species out of all genera of Winteraceae.

	1	2	3	4	5	6	7	8	9	10	11	12	13
Takhtajania perrieri	1	0	1	1	1	1	1	1	0	0	1	1	1
Drimys confertifolia	2	1	0	0	0	1	0	1	0	1	0	0	0
Drimys granadensis	2	1	0	0	0	1	0	1	0	1	0	1	0
Drimys winteri	2	1	0	0	0	1	0	1	0	1	0	0	1
Pseudowintera axillaris	1	0	0	1	1	1	1	1	0	0	0	1	1
Pseudowintera colorata	1	0	0	1	1	1	1	0	0	0	0	1	1
Tasmannia insipida	0	1	0	0	0	0	1	0	0	1	0	0	1
Tasmannia lanceolata	0	1	0	0	0	0	1	0	0	1	0	0	1
Tasmannia membranea	0	1	0	0	0	?	1	1	0	1	0	0	1
Tasmannia piperita	0 & 1	1	0	0	0	0	0 & 1	1	0	0 & 1	0	1	0
Zygogynum baillonii	1	0	1	1	1	1	0	1	1	1	1	?	?
Zygogynum pancheri	1	0	0	1	1	0	0	1	1	1	0	1	1
Zygogynum stipitatum	1	0	1	1	1	1	0	1	1	1	0	1	0 & 1
Zygogynum tieghemii	1	0	0	1	1	?	1	1	1	0	0	0	1
Degeneria vitiensis	2	0	0	1	0	1	0	1	1	1	1	1	1
Canella alba	1	0	0	1	0	1	1	1	0	0	1	0	0

Appendix 3. Characters used for cladistic analysis.

1. Tepal number (involucre not counted) and arrangement: (0) 0–3, whorled; (1) 4 or more, whorled; (2) spiral.
2. Involucre (congenitally united outermost tepals) in advanced floral buds (Vink, 1993b): (0) shorter than other tepals; (1) as long as or longer than other tepals.
3. Postgenital (?) union of the tepals following the involucre (Vink, 1993a): (0) absent; (1) present.
4. Tepal color (Harden, 1990; Vink, 1993a): (0) white; (1) cream or red.
5. Theca position on the filament (Sampson, 1987): (0) ± vertical; (1) ± horizontal.
6. Pollen diameter (polar axis) (Praglowski, 1979): (0) 18 μm or less; (1) 19 μm or more.
7. Carpel number per flower (Vink, 1970, Sampson et al., 1988): (0) 3 or more; (1) 1 or 2.
8. Oxalate crystals (including druses) in ovary wall: (0) absent; (1) present.
9. Sclereids in ovary wall: (0) absent; (1) present.
10. Ovule number per carpel: (0) 8 or less; (1) 9 or more.
11. Ovule length at anthesis: (0) 600 μm or less; (1) more than 600 μm.
12. Outer integument, number of cell layers commonly present: (0) 3 or less; (1) more than 3.
13. Inner integument, number of cell layers commonly present: (0) 2; (1) 3.